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The ventricular system of the pigeon brain: a scanning electron microscope study

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ABSTRACT

The fine structural features and regional differences of the ependyma in adult pigeons have been investigated by scanning electron microscopy. Pigeons of either sex were fixed with buffered glutaraldehyde (3%) and formaldehyde (0.5%) by intravascular perfusion. The brain was dissected using section planes adequate to expose each part of the ventricular system. The specimens were then dehydrated, critical point dried and sputtered with gold. Depending upon the distribution of cilia, microvilli and single cilia, different areas were recognised in the 4 ventricles. The topographic locations of these areas were determined using the atlas of Karten & Hodos (1967). The medial surfaces of the 1st and 2nd lateral ventricles are more densely ciliated than the lateral surfaces. In the floor of the 4th ventricle the medial part is less ciliated than the lateral parts. The circumventricular organs (subseptal organ, organum vasculosum of the lamina terminalis, infundibulum, choroid plexus, subcommissural organ, area postrema) show very characteristic surfaces and are surrounded by a transitional zone with the nonspecialised ependyma. In contrast, in the paraventricular organ the transition to the nonspecialised ependyma is rather abrupt. The ependyma covering the trochlear nucleus appears densely ciliated, differing from that of the classic circumventricular organs. Finally, the existence of openings in the caudal medullary velum, which represent direct communications between the ventricles and the subarachnoid space, was demonstrated.

INTRODUCTION

The cerebral ventricles and the central canal of the spinal cord are lined by the ependyma, a ciliated, low columnar epithelial layer which is in contact with the cerebrospinal fluid (CSF). This epithelium is interrupted at intervals throughout the ventricular system where the choroid plexus and the circumventricular organs (CVO) are located. The introduction of scanning electron microscopy (SEM) has greatly facilitated the study of the ependymal surface. Cellular surface profiles such as microvilli, cilia, blebs and single cilia are common in ependymal cells, although they are not evenly distributed. Regional differences in ependymal structure have been described in several species (Leonhardt, 1980). Such ependymal regions tend to show a precise topographic localisation and to maintain a more or less close relation with certain periventricular structures. These differences in ependymal structure may be functionally important. Studies with tracers such as horseradish peroxidase injected into the CSF spaces, particularly into the cerebral ventricles, have shown evident permeability of the ependyma to these tracers, depending on the location (Kobayashi et al. 1972; Delorme et al. 1975; Jakoubek & Tykva, 1978).

Pigeons are widely used in behavioural studies in which, in addition to other strategies, the CSF is employed as a pathway for the administration of bioactive substances (Delius et al. 1976; Deviche & Delius, 1981). Previous SEM studies in this species have revealed the existence of structural differences in the lining of the lateral ventricle (Mestres et al. 1985). In the present paper we report SEM observations on the morphology of the ventricular system and medullary velum with particular emphasis on the presence of regional differences in the surface of the ependyma and on the existence of supraependymal structures.

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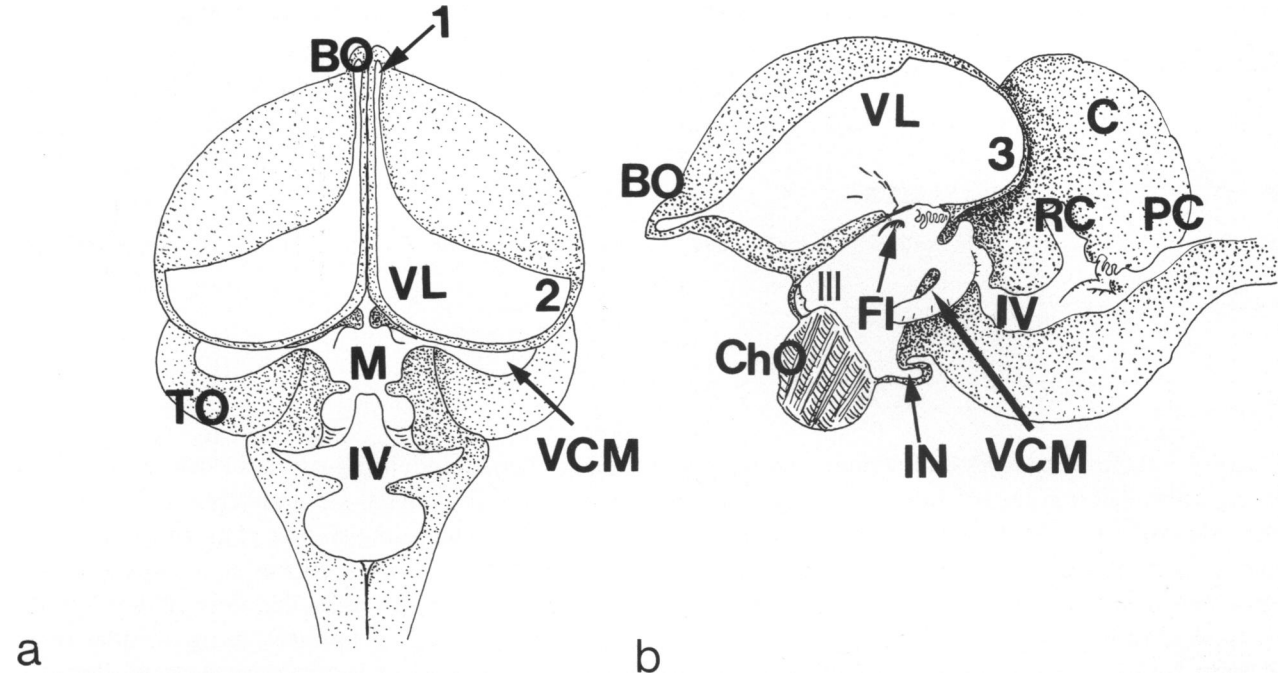

Fig. 1. Diagrammatic overviews of the ventricular system of the pigeon. (*a*) Dorsal, and (*b*) median-paramedian views. The ventricles are drawn as clear spaces. BO, Olfactory bulb; C, cerebellum; ChO, optic chiasma; FI, interventricular foramen; IN, infundibulum; IV, 4th ventricle; LT, lamina terminalis; M, mesencephalon; PC, choroid plexus; RC, cerebellar recess; TO, optic tract; VCM, mesencephalic tectal ventricle; VL, lateral ventricle; 1, medial horn; 2, lateral horn; 3, posterior horn; III, 3rd ventricle.

MATERIAL AND METHODS

Twelve adult pigeons (*Columba livia*) of either sex, purchased from a certified supplier, were used for this study. They were housed in an air-conditioned room and supplied with standard pigeon food and water ad libitum. The birds were anaesthetised with Equithesin (10% chloral hydrate, 2% sodium pentobarbital, 5% magnesium sulphate in 10% ethanol) (0.4 ml/100 g^{-1} body weight) prior to transcardiac perfusion. The vascular system was rinsed with a small amount of physiological solution (0.12 M phosphate, 0.87% NaCl) at pH 7.35 before being perfused with a buffered mixture of 3% glutaraldehyde and 0.2% paraformaldehyde at pH 7.3. The brains were left in the cranium and stored overnight in fresh fixative at 4 °C. Tissue samples of the ventricular walls were prepared for scanning electron microscopy according to procedures described elsewhere (Mestres et al. 1985). Briefly, the brain was dissected using section planes adequate to expose each part of the ventricular system. The specimens were then trimmed, dehydrated in ethanol and critical point dried in a Polaron apparatus chamber. They were examined either in a JEOL SM35 or a Cambridge Stereoscan at 20 kV or in a CamScan at 15 kV. For topographic correlations between particular regions of the ependymal lining and underlying neural structures we consulted a stereotaxic atlas of the pigeon brain (Karten & Hodos, 1967). The anatomical nomenclature adopted in the *Nomina Anatomica Avium* (Baumel et al. 1979), converted to the English spelling, is used in this paper.

RESULTS

The ventricular system of the pigeon brain consists of 2 lateral ventricles, 1st and 2nd, and 2 unpaired ventricles, the 3rd and 4th. Badawi (1967) provided an overall view of this system of cavities in a study of serial sections and casts. The macroscopic landmarks relevant for the present description are indicated in Figure 1.

The lateral ventricle

The lateral ventricle consists of a medial horn, a rudimentary lateral horn, and a posterior horn (1, 2, and 3, in Fig. 1). The medial horn extends rostrally into an open olfactory ventricle. The ependyma of the entire olfactory ventricle is densely ciliated except for small areas where microvilli predominate (Fig. 2*a*).

The surface patterns of the ependyma of the medial walls differ from those of the lateral walls. The ependyma covering the neostriatum (lateral wall) is composed of ciliated cells arranged in irregular islands

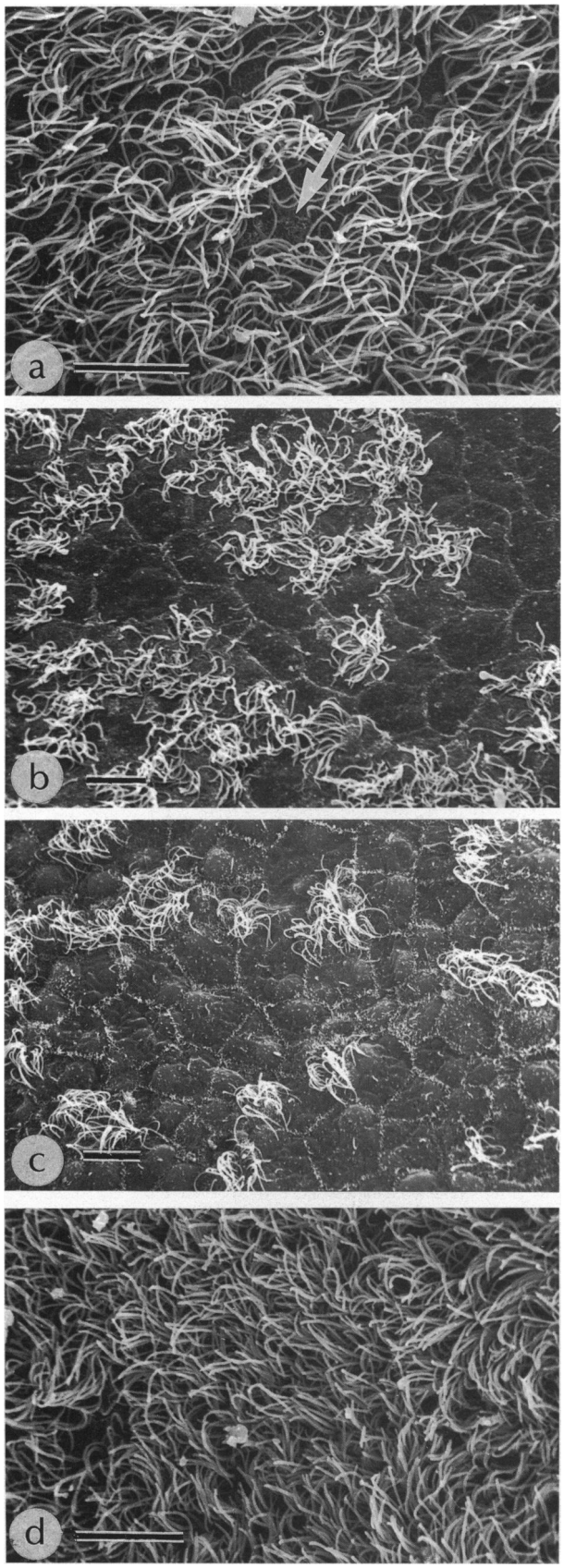

Fig. 2. Lateral ventricle. (*a*) Densely ciliated ependyma in the olfactory ventricle. Only small patches between the cilia display microvilli (arrow). Bar, 10 μm. (*b*, *c*) Heterogeneously ciliated ependyma on the lateral wall; (*b*) is located more rostral than (*c*). Bar, 10 μm. (*d*) Densely ciliated ependyma on the medial wall. Bar, 10 μm.

and cells with single cilia (Fig. 2*b*). In more posterior areas – e.g. over the ventral hyperstriatum – cilia are present only in more or less isolated tufts (Fig. 2*c*). This means that the number of cilia decreases in a rostral to caudal direction. Cells with single cilia are usually distinctly demarcated by a fringe of microvilli at their borders. Most areas of the lateral walls therefore resemble marquetry. In contrast, the ependyma of the medial wall of the lateral ventricle, i.e. that covering the septomesencephalic tract, the septum and the hippocampus, is at least as densely ciliated as the olfactory ventricle (Fig. 2*d*).

Supraependymal elements, whether free cells or nerve fibres, are an extremely rare finding in the lateral ventricle (not shown).

At low magnification the surface of the choroid plexus appears extremely folded, much the same as in the 3rd ventricle (Fig. 3*a*). Countless thin microvilli are homogeneously distributed on slightly convex apical poles, whereas the cilia usually arise from the borders of the cells (Fig. 3*b*). Epiplexus (Kolmer) cells can be found scattered on the folds of the plexus (Fig. 3*c*).

The 3rd ventricle

The most noteworthy macroscopic details of this ventricle are (1) the preoptic recess, which is an expansion at the rostral angle of the optic chiasma, (2) the infundibular recess, which is located caudal to the optic chiasma and extends into the neurohypophysis, and (3) the choroid plexus, which closes the caudal third of the roof of the ventricle (for a general topographic orientation, see Fig. 1*b*). Most of the ventricle is lined by densely ciliated ependyma. This homogeneous carpet of cilia abruptly lessens in density in the vicinity of the infundibular recess and thins out around the circumventricular organs located in this ventricle.

The subseptal organ. This lies immediately ventral to the interventricular foramen and corresponds to the mammalian subfornical organ (Fig. 4). At low magnification it can easily be recognised as an oblong area of ependyma almost entirely free of bundles of cilia and with a ridge in its dorsal half (Fig. 5*a*, *b*). The ependyma of the subseptal organ is continuous with that of the choroid plexus and shows a surface structure which resembles that of the lateral ventricles.

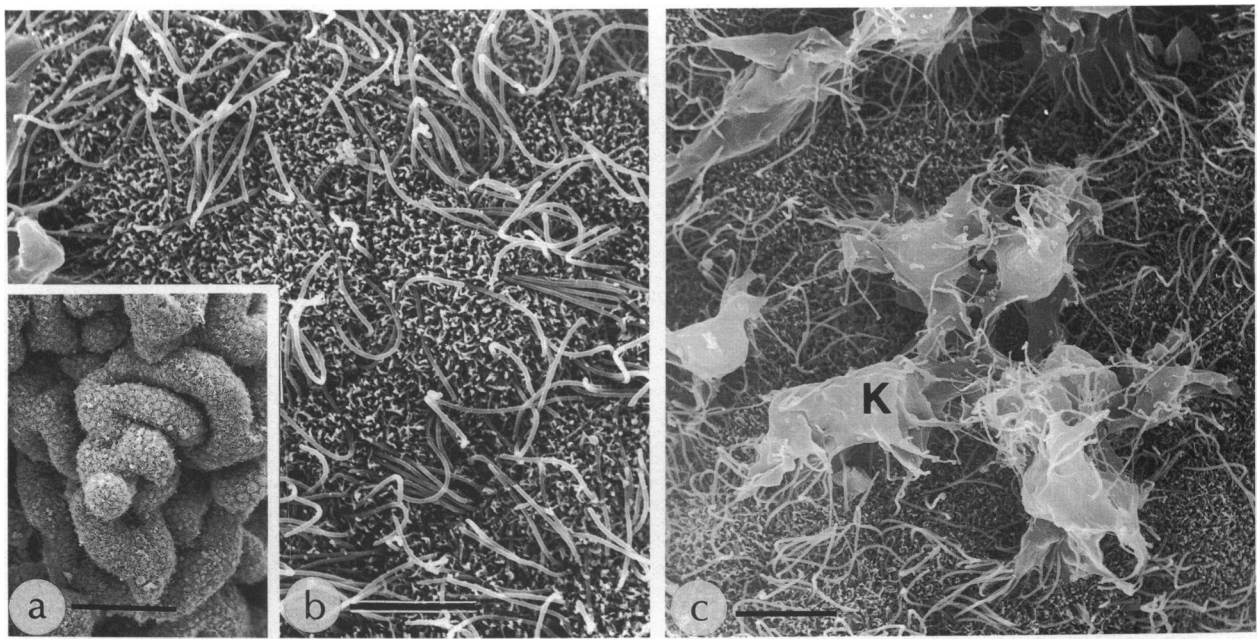

Fig. 3. Choroid plexuses (PC). (*a*) Inset. Overview of the choroid plexus in the anterior part of the 3rd ventricle. Bar, 100 μm. (*b*) Detail of the PC. Note numerous microvilli and more or less peripheral position of the cilia. Bar, 3 μm. (*c*) Kolmer cells (K) on the PC. Bar, 4 μm.

Most ependymocytes have their borders clearly demarcated by numerous microvilli. The cilia are short. Scattered among these cells are others bearing bundles of cilia (Fig. 5*c*, *d*). In the subseptal organ itself the microvilli are very abundant and cell boundaries can no longer be recognised. The single cilia here are shorter than those of the ciliated ependyma (Fig. 5*d*). The ependyma at the ventral transition zone and over the anterior commissure is also predominantly of the nonciliated type, but scattered bundles of cilia can be found (Fig. 5*e*).

The organum vasculosum of the lamina terminalis. Below the anterior commissure lies the narrowest part of the anterior wall, occupied by the organum vasculosum (Fig. 4). Most ependymal cells over this organ bulge slightly into the ventricular lumen, giving the area as a whole the appearance of a cobblestone surface (Fig. 6*a*). On closer inspection, the cells have numerous irregular profiles such as microvilli, protrusions of various sizes, and single cilia. However, bundles of cilia are not usually found on the organum vasculosum. There are also a few supraependymal cells (Fig. 6*b*).

Below the organum vasculosum the anterior wall becomes thinner and broader. This part, the most ventral portion of the lamina terminalis, extends down to the optic chiasma (Figs 4, 6*c*). In this area the ependymal cells are flatter than those of the organum vasculosum and bear microvilli and blebs; most have short single cilia (Fig. 6*d*). The contours of the ventricle in the region of the optic chiasma are characterised by 2 lateral outpocketings separated medially by a distinct crest (Fig. 6*c*, *e*). The number of ciliated cells here gradually increases in the caudal direction (Fig. 6*c*, *f*).

The infundibulum. Three types of apical pole are identifiable in the ependymal cells of the infundibular recess, listed here in the order of their frequency: (1) those with microvilli, small blebs and single cilia; (2) those with a head-like structure; and (3) those with a bundle of cilia. The 1st type is widely distributed and corresponds to the tanycytes. The 2nd is peculiar to this part of the ventricular system: the apical head-like structures either have a smooth surface and a single cilium or a 'knobbly' surface (Fig. 7*a*). It is difficult to determine whether any cilia are present in the 2nd type (compare *b*, *c* and *d* in Fig. 7). The 3rd type belongs to the common ependymocytes which are interposed between the tanycytes. Supraependymal cells but not supraependymal nerve fibres were observed in the infundibular recess (Fig. 7*e*).

The general pattern of the ependyma in the infundibular recess continues down to the entrance to the neurohypophysis (Fig. 8*a*) but the number of head-like structures and cells with bundles of cilia gradually decreases. The ependyma of the median eminence lacks them completely; its surface undulates slightly and is characterised by numerous single cilia and large, more or less spherical protrusions (Fig. 8*b*, *c*). The ependyma within the neurohypophysis appears to be constituted of cells with polygonal apical poles, most of which bear microvilli (Fig. 8*d*).

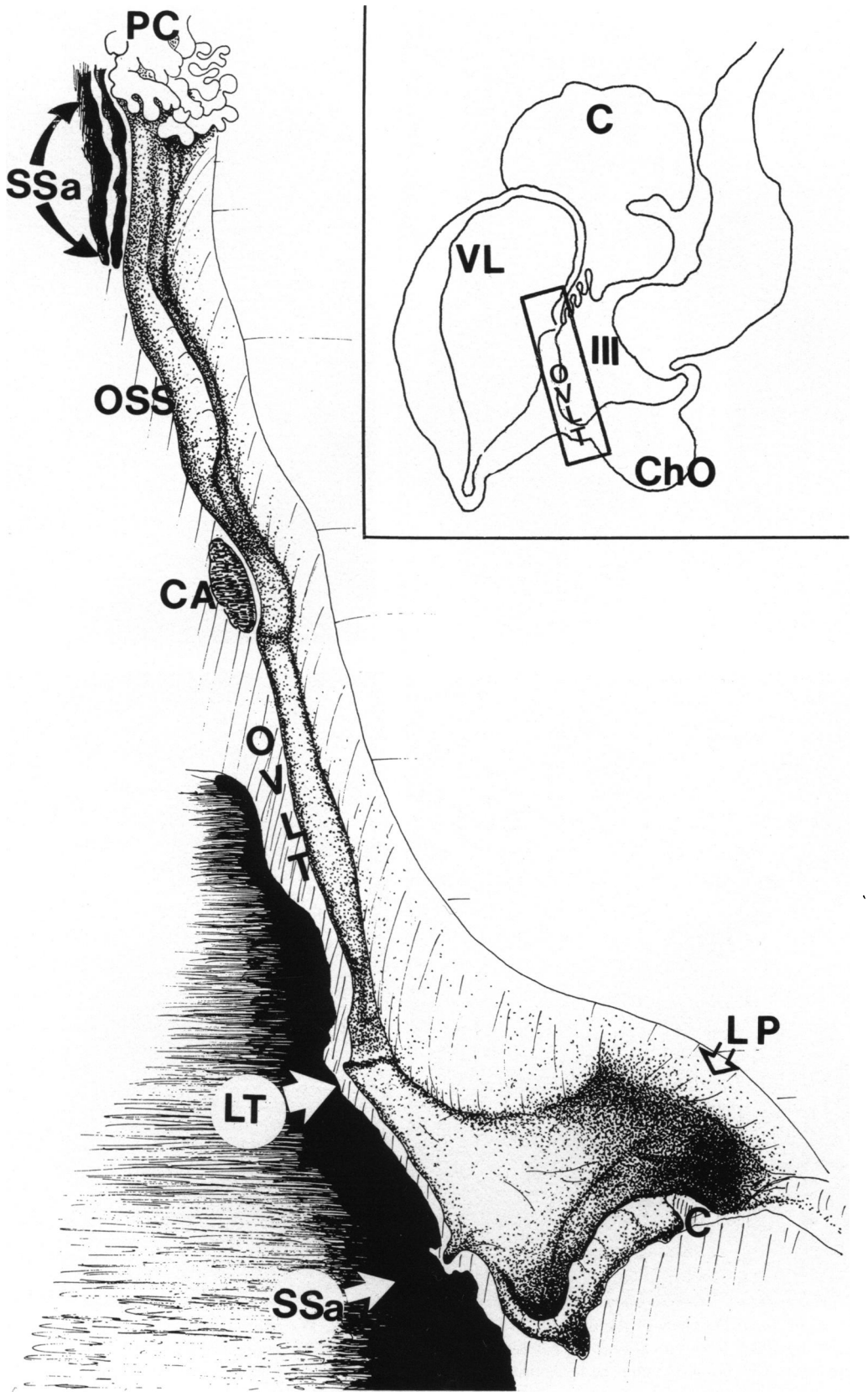

Fig. 4. Overview of anterior wall of the 3rd ventricle from the choroid plexus at the top to the optic chiasma at the bottom. PC, choroid plexus; OSS, subseptal organ; CA, anterior commissure; LT, lamina terminalis; OVLT, organum vasculosum of the lamina terminalis; C, crest on chiasma; LP, lateral pouch; SSa, subarachnoid space. Insert: the square indicates the localisation and orientation of the anterior wall of the 3rd ventricle represented in the diagram (see caption for Fig. 1).

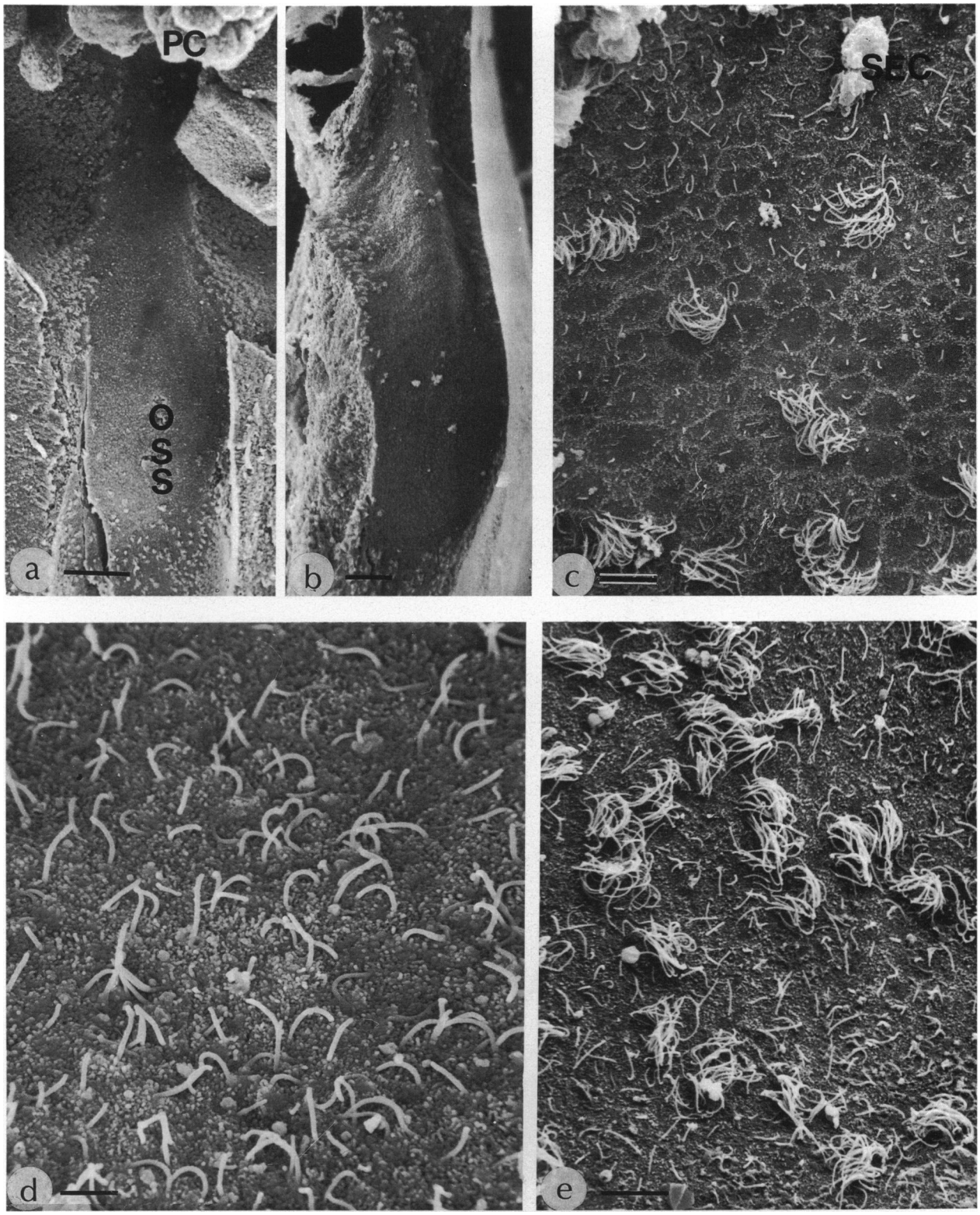

Fig. 5. Subseptal organ. (*a*, *b*) Overview of the organ at 2 different degrees of tilt. PC, choroid plexus. Bars, 100 μm. (*c*) Ependyma at dorsalmost extent of the organ. Note similarity to the pattern in the lateral ventricle. SEC, supraependymal cell. Bar, 10 μm. (*d*) Ependyma over middle of the organ. Cell borders cannot be recognised. Bar, 5 μm. (*e*) Ependyma at ventralmost extent of the organ. Bar, 10 μm.

A few also bear a bundle of cilia (Fig. 8*e*). No notable differences were observed between the ependyma of the dorsal and ventral walls of the hypophyseal recess.

The paraventricular organ. An elongated region in the lateral walls of the 3rd ventricle (Fig. 9*a*) has a unique surface profile. It marks the location of the paraventricular organ. The dorsoventral extent of the region measures 0.8–0.9 mm and it is 50–70 μm in

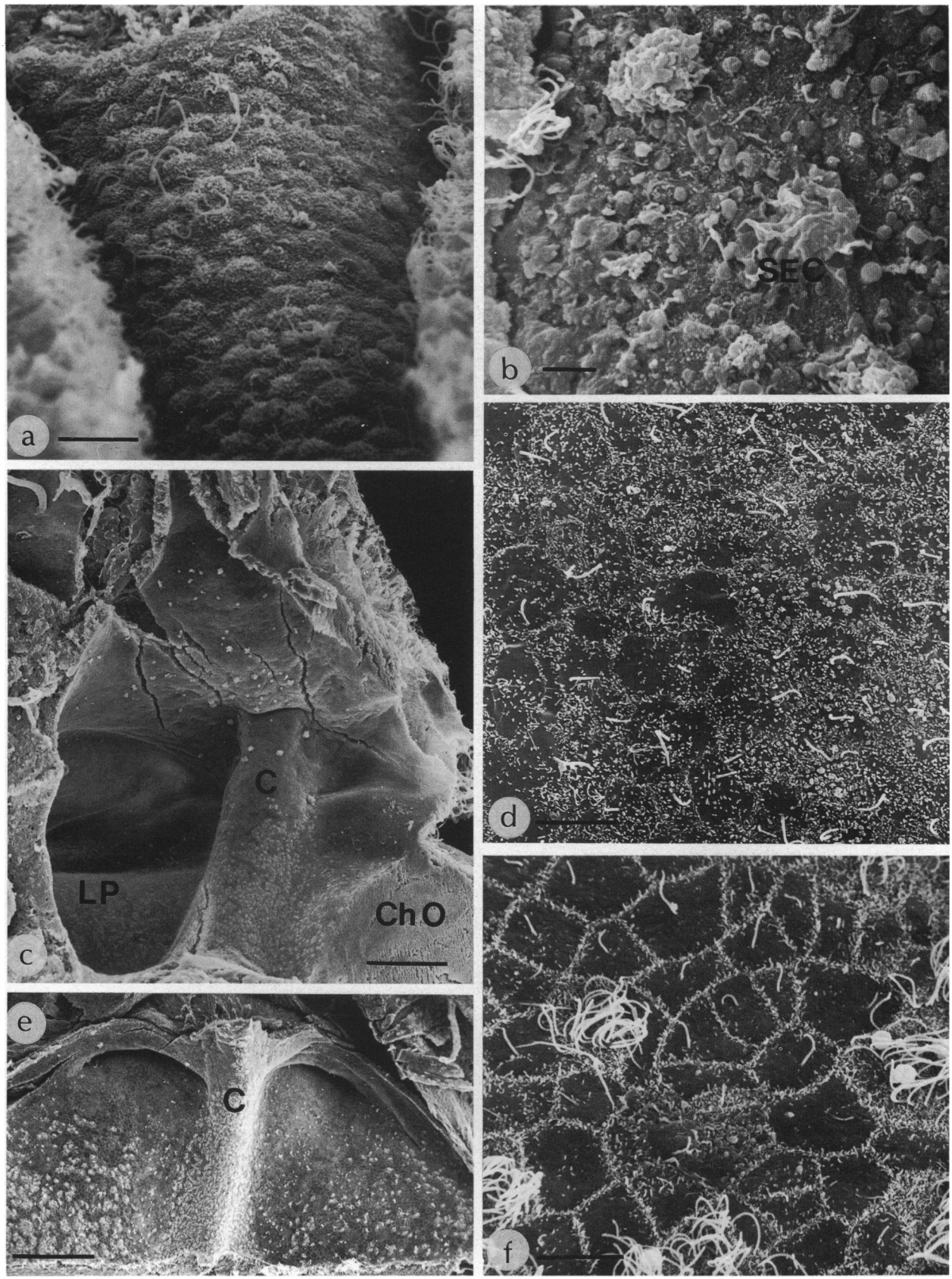

Fig. 6. Organum vasculosum of the lamina terminalis (OVLT) and the suprachiasmatic crest. (*a*) Overview of the OVLT seen caudally. Note sparse ciliation and marked 'cobblestone' effect of the surface. Bar, 10 μm. (*b*) Detail of surface of OVLT with supraependymal cells (SEC). Bar, 5 μm. (*c*) Overview of the suprachiasmatic recess looking towards the lamina terminalis. Note prominent median crest (C). ChO, optic chiasma; LP, lateral pouch. Bar, 200 μm. (*d, f*) Two examples of ependymal patterns in the lateral parts of the suprachiasmatic recess. Bars, 10 μm. (*e*) Overview of suprachiasmatic recess looking vertically at the crest (C). LP, lateral pouch. Bar, 200 μm.

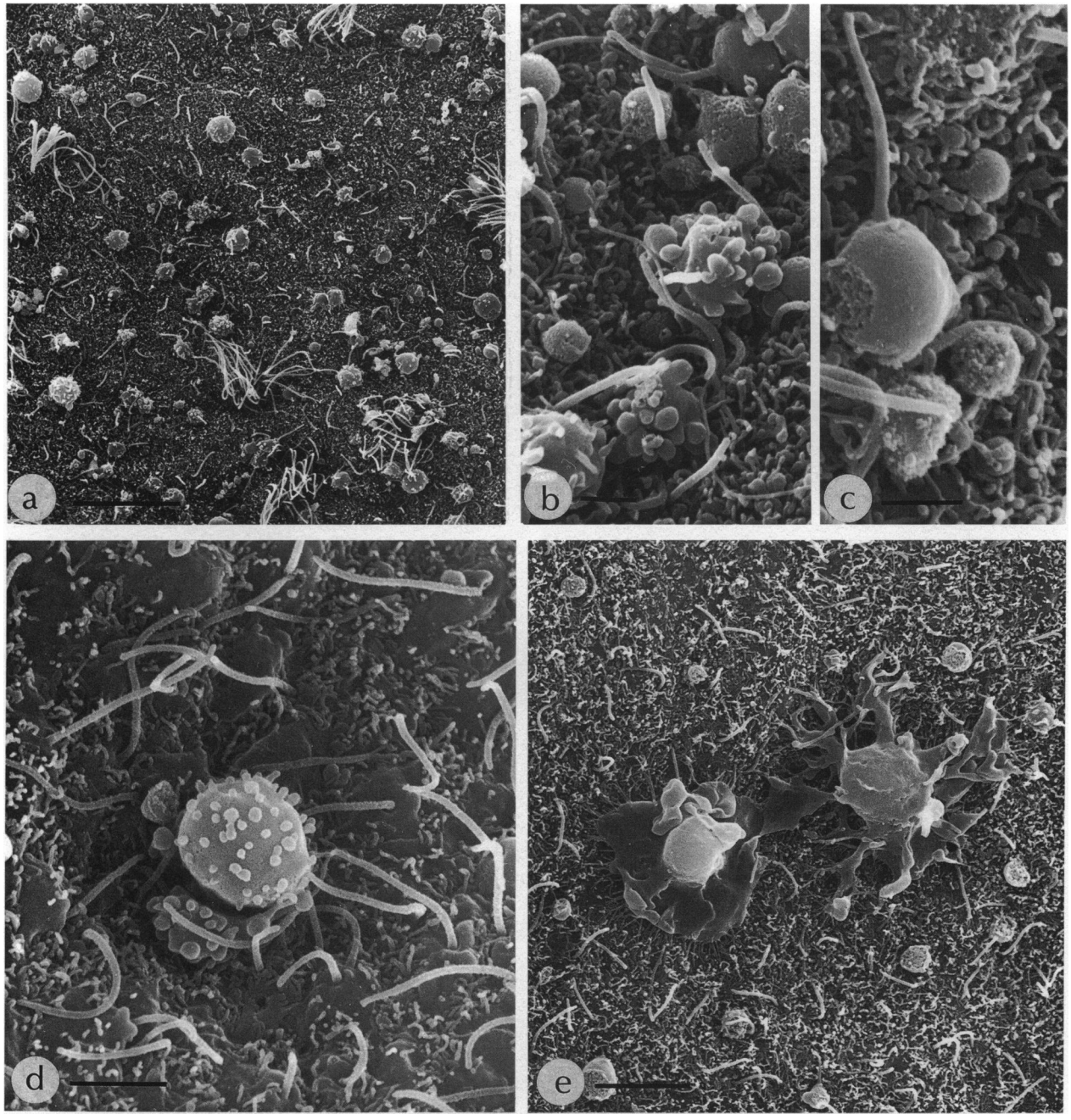

Fig. 7. Details of the ependyma of the mediobasal hypothalamus. (*a*) Lateral wall with numerous head-like structures. Bar, 10 μm. (*b*) Raspberry-like CSF-contacting neuronal processes. Bar, 1 μm. (*c*) Smoother CSF-contacting neuronal process with cilium. Bar, 1 μm. (*d*) Large CSF-contacting neuronal process with short microvilli. Bar, 2 μm. (*e*) Supraependymal cells on lateral wall of infundibular recess. Note broad lamellar processes as well as delicate filopodia. Bar, 2 μm.

width. The ventricular surface of the organ is a zone of juxtaposed globular apical cellular poles that protrude into the ventricle. The transition from the paraventricular organ to the normal ciliated ependyma is abrupt (Fig. 9*b*). The globular protrusions vary in diameter from 0.9 to 1.8 μm. Some are entirely smooth; others bear short finger-like extensions and small bleb-like appendices. They are so closely packed that no free spaces can be seen between them (Fig. 9*c*, *d*, *e*). Bundles of cilia are present only in marginal areas. Neither nerve fibres nor supraependymal cells were observed in the region of the paraventricular organ. In some instances (Fig. 9*c*) the globules were damaged during dissection so that the plasma membrane was lost, revealing elements of the cytoplasm.

The subcommissural organ

The ependyma at the transition zone from the 3rd ventricle to the mesencephalic aqueduct displays

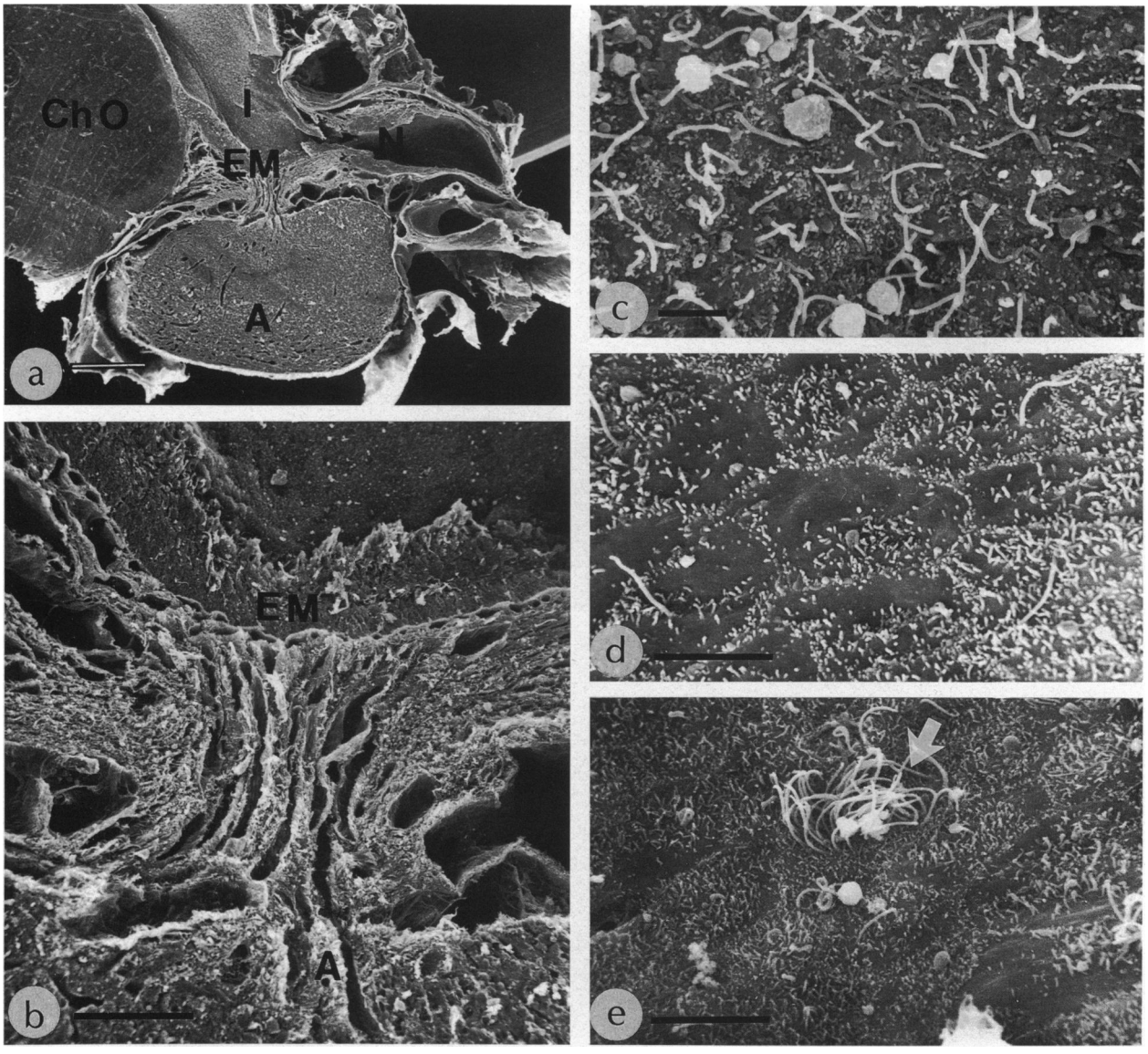

Fig. 8. Infundibulum – hypophysis. (*a*) Overview of infundibular recess (I) which continues into the neurohypophysis (N). A, adenohypophysis; ChO, optic chiasma; EM, median eminence. Bar, 400 μm. (*b*) Detail of (*a*). Portal vessels extending between median eminence (EM) and adenohypophysis (A). Bar, 100 μm. (*c*) Surface of median eminence. Bar, 5 μm. (*d*) Dorsal wall of neurohypophyseal recess. Bar, 10 μm. (*e*) Ventral wall of neurohypophyseal recess. The ependymal cells only rarely have bundles of cilia (arrow). Bar, 10 μm.

differences between its dorsal and ventral surfaces. The ventral surface consists only of common, evenly ciliated ependyma covering the shallow groove of the median sulcus. The sulcus continues along the floor of the aqueduct and into the 4th ventricle. The dorsal surface, however, consists of a distinct type of ependyma covering the posterior commissure that corresponds to the subcommissural organ.

The ventricular surface of the subcommissural organ extends in a rostrocaudal direction, covering the anterior and inferior aspects of the posterior commissure (Fig. 10*a*). It is approximately 0.7–0.8 mm long and 0.1–0.2 mm wide. The subcommissural organ is framed by an irregularly ciliated crest. This crest is particularly prominent in the anterior part of the organ and resembles a fold of ependyma. In this area the crest has fewer cilia but numerous supraependymal cells and a few supraependymal nerve fibres (Fig. 10*b*). Over the organ itself the cilia are fairly evenly distributed and spaced far enough apart so that remarkably long microvilli covering the apical poles can be seen. Moreover, a more or less fine filamentous material can be observed strung on and between the ends of the cilia and extending in rostrocaudal direction (Fig. 10*c*). This fibre may be very long and can be followed until it leaves the ventricular system at the entrance to the central canal (Fig. 13*f*). The irregularly ciliated crest

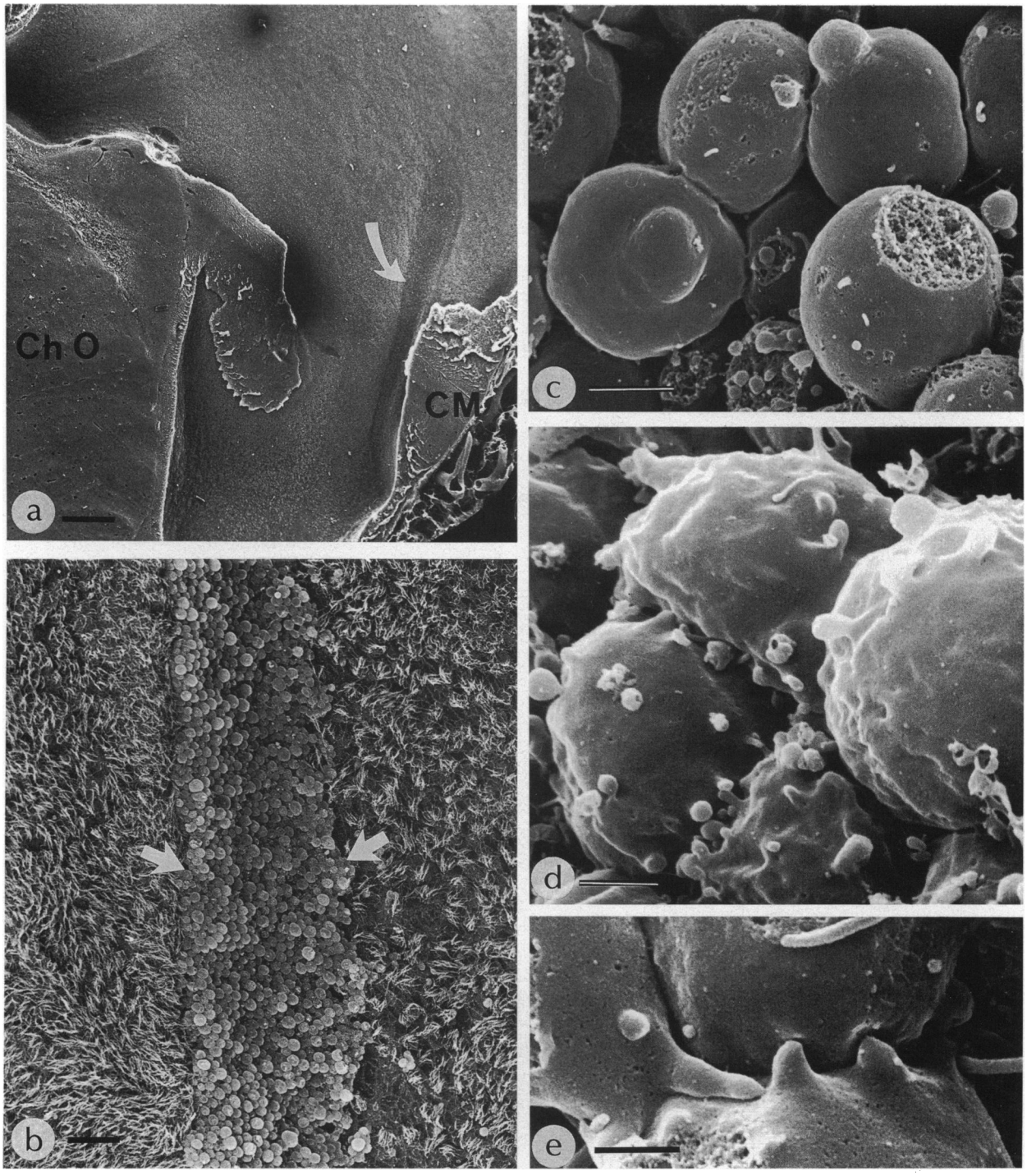

Fig. 9. Paraventricular organ (OPV). (*a*) Overview of lateral wall of 3rd ventricle with area including OPV. ChO, optic chiasma; CM, mamillary body. Bar, 200 μm. (*b*) The OPV (arrows) is completely surrounded by more or less densely ciliated ependyma. Bar, 20 μm. (*c*) Several spherules of the OPV. They bear protrusions, some of which appear to have been damaged during dissection. Bar, 2 μm. (*d*) Spherules that have small bleb-like protrusions. Bar, 1 μm. (*e*) Detail of spherules that have more finger-like protrusions. Bar, 1 μm.

framing the subcommissural organ laterally represents the transition zone to the surrounding densely ciliated nonspecialised ependyma. Neither supraependymal cells nor nerve fibres were found in these areas (Fig. 10*d*).

The mesencephalon

The ventricular spaces within the mesencephalon are the aqueduct and the tectal ventricles which extend laterally from the rostral part of the aqueduct (Fig. 1*a*, *b*). The ventral surface of the aqueduct is as

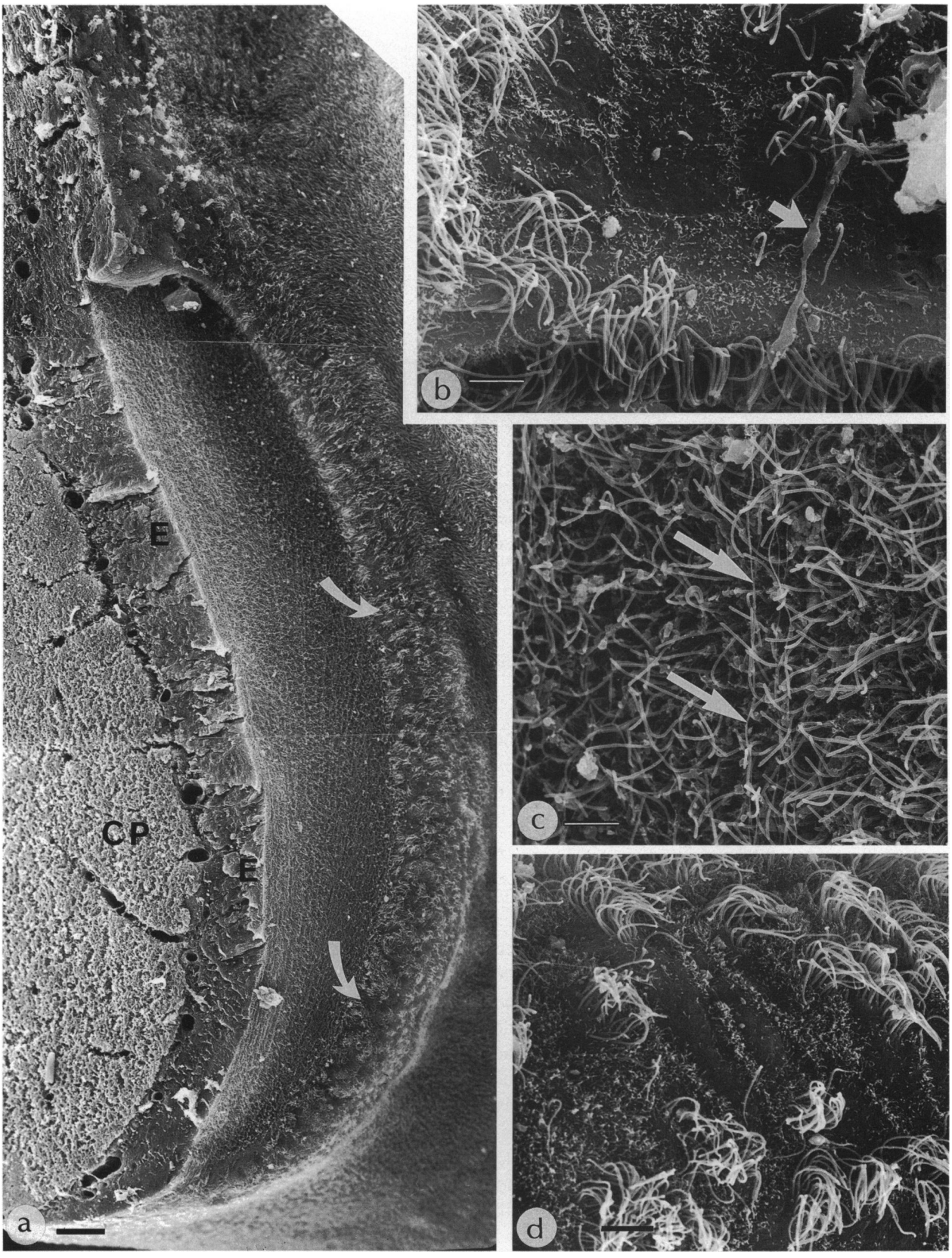

Fig. 10. Subcommissural organ (OSC). (*a*) Overview of the OSC seen from below. The top of the micrograph is rostral. CP, posterior commissure; E, cut surfaces of ependymal cells; arrows, crest. Bar, 30 μm. (*b*) Supraependymal fibre (arrow) in area immediately rostral to the OSC. Bar, 3 μm. (*c*) Detail of surface of the OSC. Note delicate fibrils of secreted substance (arrows) between the cilia. Bar, 3 μm. (*d*) Mosaic pattern of cell surfaces on crest at lateral borders of the OSC. Bar, 4 μm.

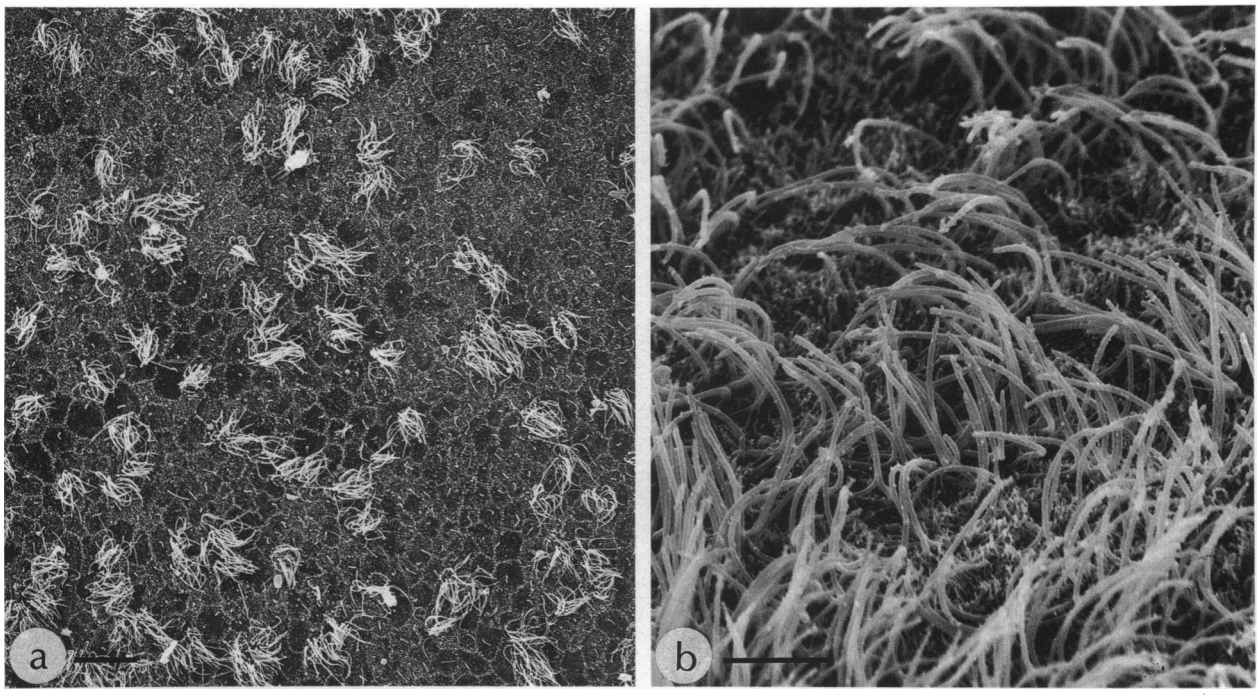

Fig. 11. Mesencephalon – tectal ventricle. (*a*) Ependyma at dorsal midline immediately caudal to the posterior commissure. Note variable distribution of cilia and microvilli. Bar, 10 μm. (*b*) Detail of ependyma within the tectal ventricle. The cells are densely covered with microvilli and the cilia are distributed irregularly. Bar, 2 μm.

densely ciliated as it was beneath the subcommissural organ. The median aspect of the roof of the aqueduct, however, has a very heterogeneous pattern for the distribution of cilia and microvilli (Fig. 11*a*). The ependyma within the tectal ventricles is irregularly ciliated but evenly covered with microvilli (Fig. 11*b*). Cell borders remain obscured.

The 4th ventricle

After the aqueduct has narrowed at the so-called isthmus, the transition into the 4th ventricle is quite abrupt (Fig. 1*a*, *b*). When the cerebellum has been removed, the ventricular floor can be recognised. The calamus scriptorius is prominent, particularly at the level of the trochlear nuclei (Fig. 12*a*). Both the floor and the sides of the calamus scriptorius are densely ciliated at this level (Fig. 12*b*, *c*, *d*). Supraependymal structures were not seen in this area.

In median sagittal preparations the cerebellar ventricle can be scanned (Fig. 13*a*). It is lined with ependyma bearing a dense coat of microvilli and loosely distributed bundles of cilia (Fig. 13*b*). No differences in the distribution of profiles were seen from one part of the ventricle to the next.

The floor of the 4th ventricle which covers the medial longitudinal fasciculus has a very heterogeneous pattern (Fig. 13*c*). Parallel paths of ciliated cells can be followed along the calamus scriptorius until it disappears into the central canal (Fig. 13*d*, *e*). Laterally, cells bearing bundles of cilia occur singly or in groups and are separated by areas with cells lacking cilia but marked by microvilli at their borders (Fig. 13*d*, *e*, *f*). This pattern is reminiscent of that seen on the lateral walls of the lateral ventricles.

In most specimens Reissner's fibre was a prominent feature on the floor of the 4th ventricle (Fig. 13*f*). Supraependymal cells were also occasionally seen on the ventricular floor but nerve fibres were not found (Fig. 13*g*). The choroid plexus fills much of the ventricular lumen (Fig. 13*a*). Its surface ultrastructure resembles that of the plexuses in the other ventricles. Laterally the ependyma of the 4th ventricle covers the cerebellar peduncles and, caudally, the vestibular nuclei. The ependymal pattern in these areas is much the same as in the lateral ventricle with patches of ciliated and nonciliated cells.

The area postrema. A broad arc of ependyma at the posterior brim of the 4th ventricle has an entirely different pattern from that seen in other areas of this ventricle. This ependyma belongs to the area postrema (Figs 13*c*, 14*a*). The apical poles of the cells are more or less oblong and protrude slightly into the lumen of the ventricle (Fig. 14*b*). Each bears a single long cilium and a few very short microvilli. As a rule, the

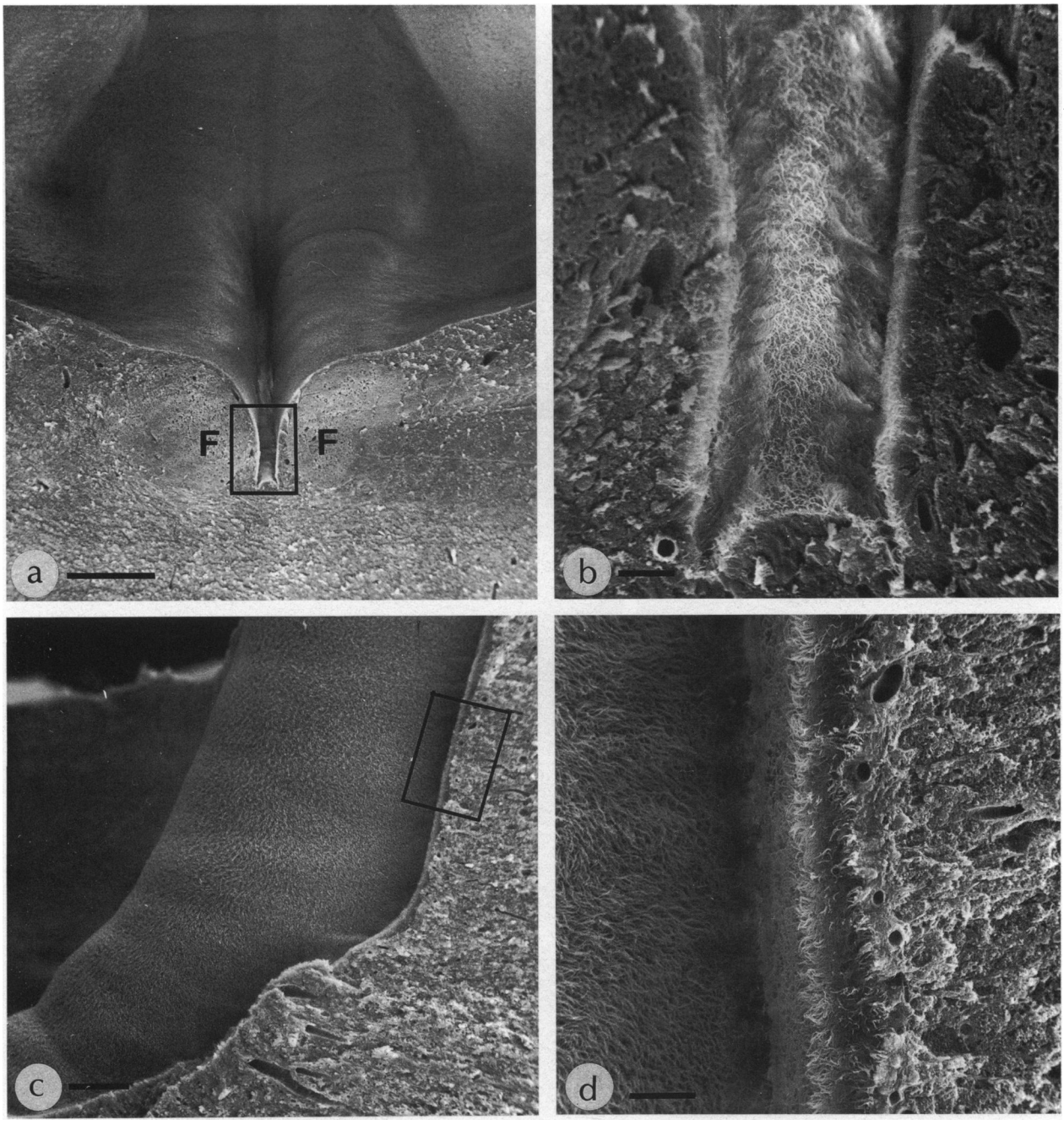

Fig. 12. Trochlear recess. (*a*) Overview of the trochlear area of the 4th ventricle seen rostrally. F, medial longitudinal fasciculus. Frame indicates location of micrograph (*b*). Bar, 100 μm. (*b*) Detail of ependyma in trochlear area. Note dense ciliation. Bar, 20 μm. (*c*) Trochlear area viewed from the midline. Note uniform dense ciliation. Frame indicates location of micrograph (*d*). Bar, 100 μm. (*d*) Detail of (*c*). Bar, 40 μm.

surface of the area postrema is uneven although occasional flat cells with few microvilli can be found in the median parts above the entrance to the central canal (Fig. 14*c*). Small depressions surrounded by distinctly protruding cells can be found more laterally (Fig. 14*d*). There were no supraependymal elements in the area postrema.

The caudal medullary velum. The velum is an expanse of extremely thin tissue extending from the choroid plexus, which spans the ventricle below the cerebellum, to the caudal rim of the area postrema (Figs 13*a*, 15*a*). In order to view the ventricular side of the velum it was detached from the choroid plexus and gently folded caudalward after critical point drying. Manipulation after critical point drying caused numerous tears in the velum, but large areas remained intact. The ependymal cells were usually quite convex, round to oblong, and some had single

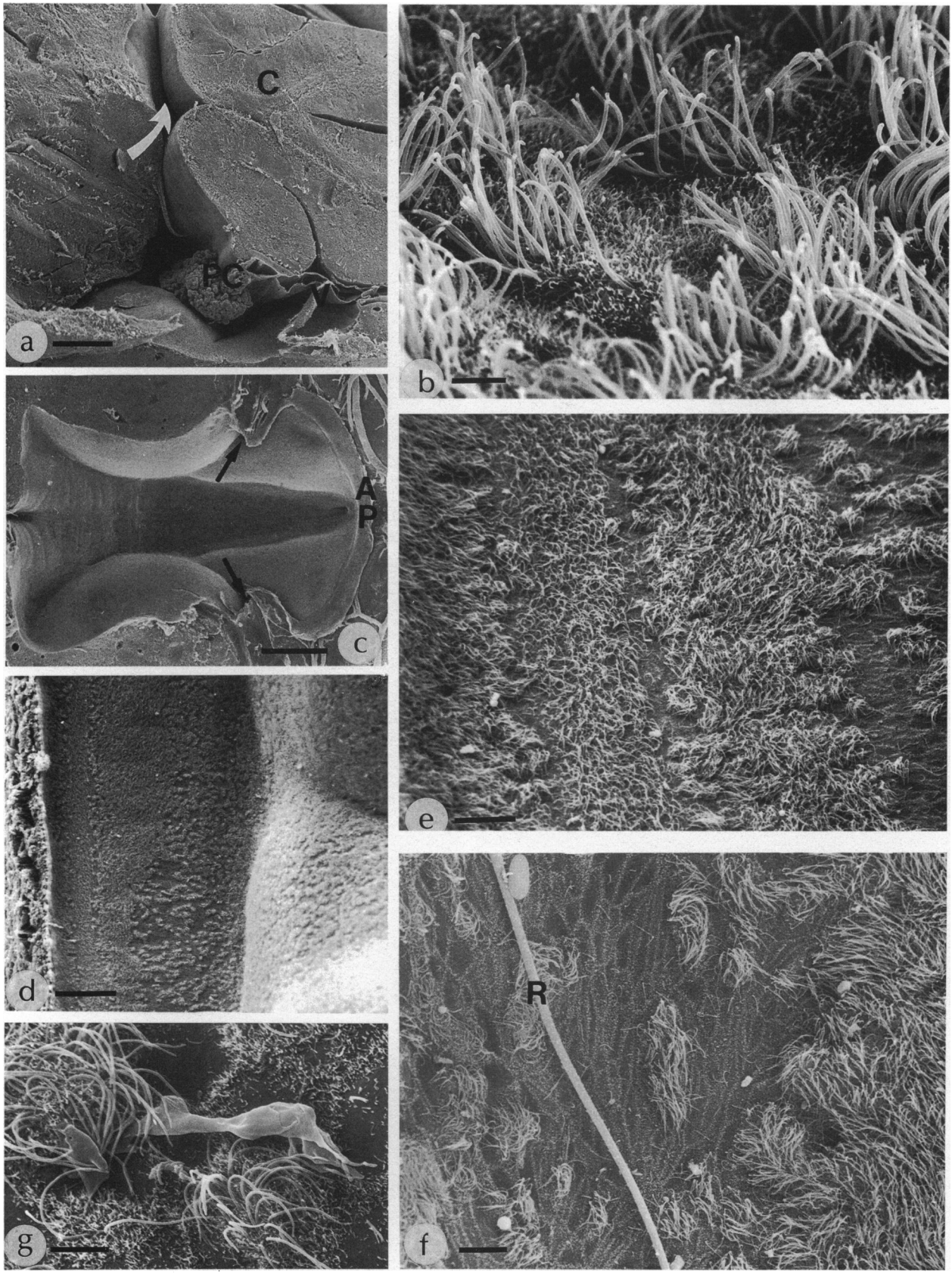

Fig. 13. Fourth ventricle. (*a*) Overview of 4th ventricle in median sagittal section. Rostral is to the left. Cb, cerebellum; arrows, cerebellar recess; PC, choroid plexus; V, medullary caudal velum. Bar, 500 μm. (*b*) Ependyma in dorsal aspect of the cerebellar recess. Note dense covering of long microvilli and distinctly separated bundles of cilia. Bar, 3 μm. (*c*) Overview of floor of 4th ventricle. Area postrema (AP) at right. Arrows, lateral recess. Bar, 500 μm. (*d*) Middle third of floor of 4th ventricle. Note regular paths of cilia in midline (left) and irregularly scattered bundles of cilia more laterally (midsection of micrograph). Bar, 100 μm. (*e*) Detail of (*d*) showing median paths of cilia.

cilia. The microvilli were more like tiny knobs and were very irregularly dispersed.

Within the intact areas several groups of pores or fenestrations of various sizes were found. They extended through the ependymal layer and its external lining of pial tissue (Fig. 15*b*, *c*). The edges of the pores showed no signs of mechanical stress. In size they ranged from only a few μm to ~ 100 μm across.

DISCUSSION

The nonspecialised ependyma

The more or less cuboidal to squamous ependymocyte is the most common ependymal cell. Low (1982) referred to this cell type as a nonspecialised ependymocyte and the term will also be employed here. It is generally understood that nonspecialised ependyma covers all areas of the ventricles with the exception of the circumventricular organs and the choroid plexuses. Nonspecialised ependymocytes vary considerably in their apical fine structure. There are ependymocytes with numerous kinocilia and a varying number of microvilli and other ependymocytes with only single cilia and a variable number of microvilli. The uneven distribution of these 2 basic forms of ependymocyte produces regional patterns in determined areas of the ventricular walls that may be topographically significant. Three patterns were observed in the pigeon ventricles: (1) areas in which only cilia could be seen; (2) areas in which groups of cells bearing numerous cilia were scattered between cells with only single cilia; (3) areas in which microvilli predominated.

Similar patterns have been observed in some mammals, the vertebrate class so far most extensively studied by SEM (Mitchell, 1980; Ferraz de Carvalho et al. 1986). These patterns are by no means a domain of the homeothermic vertebrates. They have been studied in both teleost and cartilaginous fishes (Kotrschal et al. 1985, 1987), in a few amphibian species (McKenna & Chairetakis, 1980; Gona & Hauser, 1982), and in some reptiles (Hetzel, 1977). Ependymal areas that have relatively few cilia, or in which the surfaces of the ependymocytes are readily visible between the tufts of cilia, have been seen in mammals in association with regions of white matter. Areas in which the tufts of cilia are much more closely approximated have usually been seen in association with regions of grey matter (Hasan et al. 1978; Hetzel, 1978; Flor et al. 1979; Page et al. 1979; Torvik et al. 1981). Although some authors have observed discrepancies in this correlation between an ependymal pattern and the underlying tissue and have pointed to the difficulties encountered when extrapolating from one species to another (Scott et al. 1974), it seems generally to apply to most areas of the mammalian lateral ventricles. In pigeons, however, the ependymal patterns are evidently distributed in such a manner that the areas of white matter are covered by the most densely ciliated ependymocytes whereas the areas of grey matter are covered by ependymocytes with fewer cilia and usually fewer microvilli. In general terms, this would be almost the reverse of the mammalian pattern, at least for the lateral ventricles. The micrograph of the pigeon lateral ventricle presented by Koshiba et al. (1980) very clearly shows a pattern of the kind we found on the lateral wall of the lateral ventricle. The authors unfortunately did not state from which area of the ventricle their micrograph was taken.

The patterns seen in the nonspecialised ependyma of the pigeon 3rd ventricle resemble fairly closely those of the corresponding areas in other animals (rat: Brawer et al. 1974; Mestres & Breipohl, 1976; frog: De Waele et al. 1974). The dorsal walls of the 3rd ventricle are densely ciliated, whereas the ependymal cells covering hypothalamic areas and the circumventricular organs usually have only single cilia.

In the pigeon 4th ventricle there are again remarkable differences in surface patterns among the nonspecialised ependymocytes. The variations in the degree of ciliation that are typical of the pigeon were also seen in the chicken (Hirunagi & Yasuda, 1979*a*), but so far not in mammals (mouse: Yamadori & Yagihashi, 1975; rabbit: Leonhardt & Lindemann, 1973; rat and cat: Rascher & Mestres, unpublished). The descriptions of the ependymal patterns in the 4th ventricle that have appeared to date seem to agree that the ependymocytes of the median sulcus in birds have comparatively few cilia whereas immediately lateral to the midline there are narrow bands of densely ciliated ependymocytes and lateral to these the mosaic pattern appears. Bands of ciliated cells have also been seen in the frog cerebellum in a topographically identical location (Gona & Hauser, 1982). In mammals,

Bar, 20 μm. (*f*) In most specimens Reissner's fibre (R) is a very distinct structure lying on the floor of the 4th ventricle. Note mosaic pattern of ependymal cells. This area is slightly more lateral than that in the previous figure. Bar, 10 μm. (*g*) A supraependymal cell on the floor of the 4th ventricle Bar, 3 μm.

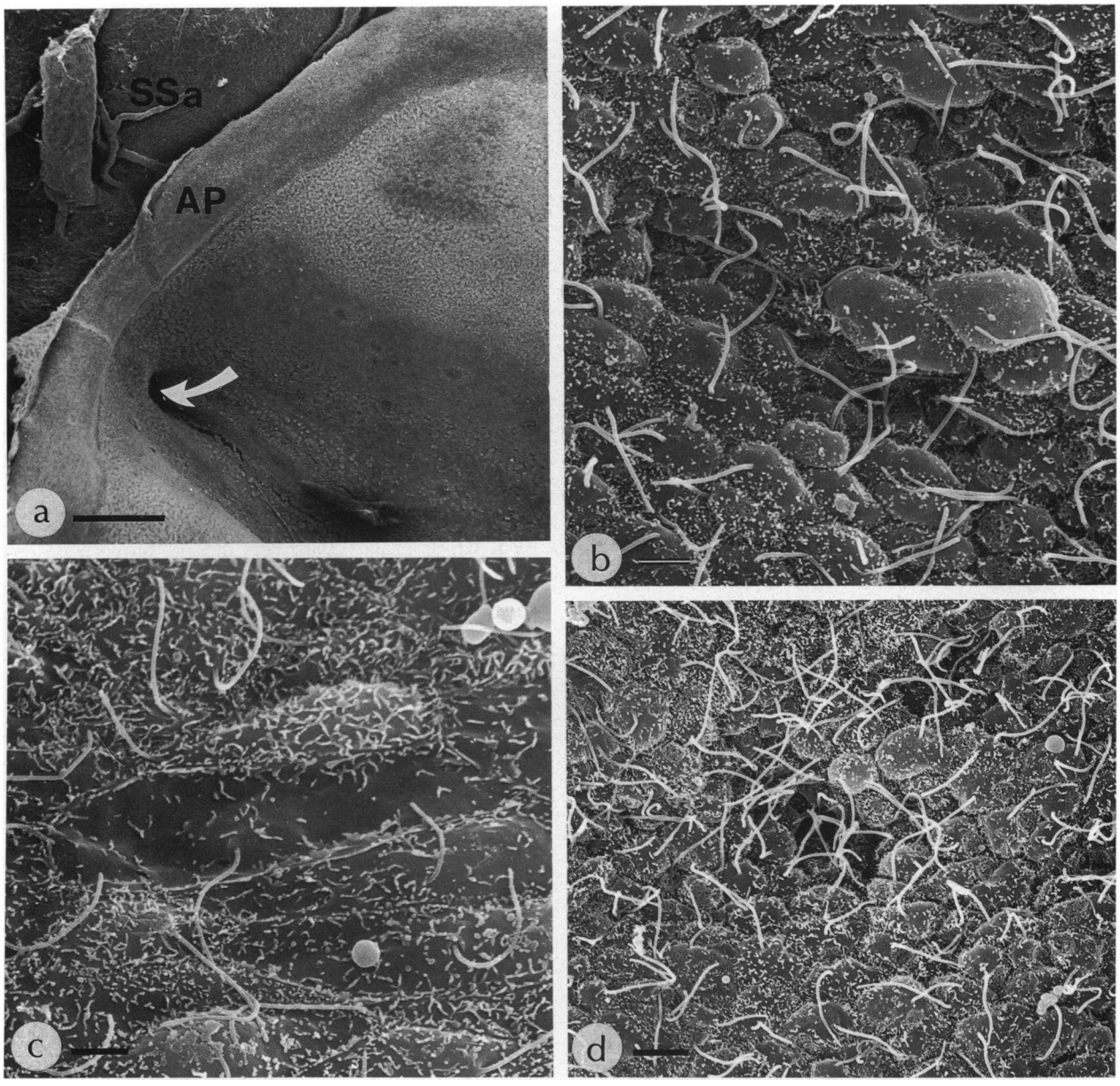

Fig. 14. Area postrema (AP). (*a*) Overview of the AP. Behind it lie blood vessels in the subarachnoid space (SSa), in front of it is the floor of the 4th ventricle with the obex (curved arrow). Bar, 200 μm. (*b*) Detail of AP. Most of its surface is characterised by this kind of 'cobblestone' pattern with single cilia. Bar, 2 μm. (*c*) Detail of AP in posteriormost part. Some cells have large, flat surfaces. Bar, 2 μm. (*d*) Pit-like indentations are an occasional finding in the AP. Bar, 3 μm.

however, ciliation is evidently uniform and rather dense throughout the 4th ventricle (Scott et al. 1974; Jacobs & Monroe, 1977).

The choroid plexus

The general appearance of the choroid plexuses in the present material closely resembles that described earlier by Koshiba et al. (1980) and is remarkably similar to that observed in the chicken (Hirunagi & Yasuda, 1979*c*: Gammal, 1981, 1983). Although these comparisons can be made only between 2 avian species, they belong to distinct orders and it might hold true for other bird species that the choroid plexus cells are characterised by cilia that are frequently located at the cell borders and by the presence of innumerable delicate microvilli. The plexus of birds differs from that of mammals with respect to the number and position of the cilia. Whereas the cilia of the pigeon plexus are scattered or even located at the periphery of the apical pole, they are, if present at all, usually bundled in the centre of the apical poles of the cells in mammals (Yamadori, 1972; Scott et al. 1974;

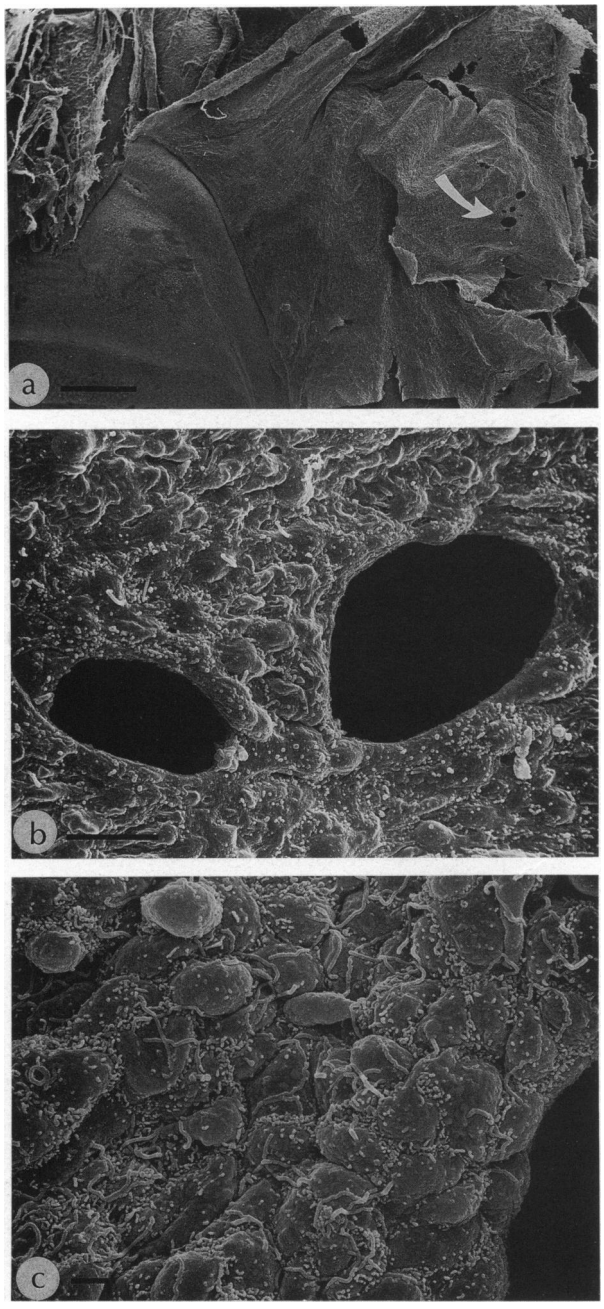

Fig. 15. Caudal medullary velum of the 4th ventricle. (*a*) Overview of the caudal medullary velum, folded backwards so that its ventricular surface can be seen. The ruptures are artefacts due to manipulation, the pores (arrow) are not. AP, area postrema. Bar, 300 μm. (*b*) Two medium-sized pores. Bar, 10 μm. (*c*) Edge of a large-sized pore. Note the 'cobblestone' pattern of the ependymal cells. Bar, 3 μm.

Peters & Swan, 1979). The functional significance of the cilia may be interpreted in connection with transport functions. Ciliary motion produces minute currents in the CSF at the apical poles of the cells and these probably lead to concentration gradients between fluid and tissue (Worthington & Cathcart, 1966; Wright, 1982; Roth et al. 1985). The microvilli represent cell membrane material involved in the uptake and release of substances into the CSF (Wright, 1982). The apical poles of the choroid plexus cells in both the pigeon and the chicken are markedly convex, a feature they have in common with the plexus cells of mammals (Low, 1982; Ling, 1983; Ling et al. 1988).

The bleb problem

In areas in which the plexus had been compressed against the wall of the ventricle the microvilli and cilia were flattened against the cell surface and the convexity of the apical poles had also been flattened. In such areas in which compression had evidently occurred, there were also numerous blebs and spherical protrusions measuring ~ 0.5 μm in diameter, whereas these were rarely found in areas that had not been compressed. In general, the morphology of these cells suggests that distinct, slender microvilli do not coexist with blebbing activity. Koshiba et al. (1980) observed large numbers of blebs and protrusions of various sizes and shapes on the plexuses of their untreated pigeons. Their methods of fixation differed from ours, however, and their medium-power micrographs show blebs to be particularly prevalent in areas in which the plexus was compressed. Our findings agree with theirs but we were not able to distinguish 3 different types of choroidal epithelial cells on the basis of blebs or protrusions.

The significance of the blebs under physiological conditions is not yet understood. Blebs should be distinguished from larger protrusions (> 2 μm in diameter) that have been described in earlier reports. We did not find any of these larger structures in our material. Koshiba's recent studies (1987*a*, *b*) showed that the plexuses are very sensitive to drugs, but the author's variations in fixation technique make precise comparisons difficult. Ling et al. (1988) revealed extensive blebbing after intracisternal injection of crotoxin. Studies in other species indicate that the appearance of blebs can be correlated with the application of certain methods of fixation. In avian species they were found after cardiovascular perfusion but never after intraventricular perfusions (Takei et al. 1978). Intraventricular fixation probably fixes the cell surfaces before they are able to react to sudden metabolic modifications that accompany cardiovascular perfusion. Similar phenomena have also been observed in mammals, not only in plexus cells, but also in other areas of the ependyma (Rodríguez, 1976). TEM studies of these protrusions in the pigeon plexus did not reveal any specific contents and

therefore it does not appear that they are an expression of secretory processes.

The subseptal organ

In birds there is no true subfornical organ because there is no fornix, but submammalian species do have a circumventricular organ in the corresponding region of the 3rd ventricle. In agreement with Kuenzel & van Tienhoven (1982) we are also using the term subseptal organ introduced by Legait & Legait (1958) (organum subseptale in the *Nomina Anatomica Avium*, 1979). The surface contours and the ultrastructural details of the pigeon subseptal organ are quite similar to those in the Japanese quail (Mikami & Asari, 1978; Tsuneki et al. 1978). Structurally, the organ can be divided into a stalk and a body in both species, a division that is also possible in most mammals examined to date (see Leonhardt, 1980, and Mitchell, 1980, for references). The ultrastructural similarities between the organ in birds (Takei et al. 1978) and mammals, however, are not very numerous, particularly if the subseptal organ is compared with the rat and cat subfornical organ. The surface pattern in the pigeon is much more uniform than in the rat and lacks the supraependymal structures found in the mammal (Phillips et al. 1974; Dellman & Simpson, 1979; Mestres et al. 1984; Rascher & Mestres, 1985). Because of the general lack of information on the subseptal organ in poikilothermic vertebrates, it is not yet possible to determine whether this circumventricular organ is structurally more like the mammalian subfornical organ or the subseptal organ of subavian species. In one frog species (Dellmann, 1978) it is apparently well supplied with various ependymal and supraependymal structures, whereas in another frog species (De Waele & Dierickx, 1979) it was seen as a 'bare area'. In mammals, the subfornical organ and in bird species other than the pigeon the subseptal organ has been found to contain receptors for angiotensin II and to be involved in the regulation of drinking behaviour (Phillips & Felix, 1976; see Dellmann & Simpson, 1979, for a review). Although there are to date no reports describing its function in the pigeon, it may be assumed to be similar to that of other birds (see Simon et al. 1987).

The organum vasculosum of the lamina terminalis

This circumventricular organ in the pigeon is also comparable to that of the quail (Mikami, 1976). The organum vasculosum of these bird species is remarkably large in its dorsoventral extent. The nonciliated ventricular region extends beyond the area comprising the neurohaemal zone (Mikami, 1976) and is proportionally larger than is found in mammals (Phillips et al. 1978). As in mammals, the apical poles of the nonciliated cells protrude significantly into the lumen of the ventricle. The organ as a whole, however, is much more crest-like in birds than in mammals. The contours of the anterior 3rd ventricle of the pigeon appear to be unique because of the voluminous lateral recesses above the optic chiasma. The organum vasculosum of both bird species appears to be a circumventricular organ which bears relatively few supraependymal structures. They are not mentioned in Mikami's study (1976) and are only an occasional finding in pigeons. Supraependymal structures such as free cells and fibres are much more frequent features in mammals (Weindl & Schinko, 1977; Card & Mitchell, 1978; Riesco et al. 1988). Reports about the functional significance of the organum vasculosum, whether in mammals or in birds, are rare. This is understandable because it is an area of the brain that cannot easily be lesioned or deafferented without causing lesions in the wealth of neighbouring nuclei and neuronal pathways.

The paraventricular organ

The paraventricular organ has so far been found only in submammalian vertebrates. Although its borders are usually clearly definable, measurements of the organ in other species are not found in the literature available to us (for an extensive general review, see Vigh-Teichman & Vigh, 1983). The most remarkable feature of the paraventricular organ is the bulbous protrusions found at its ventricular surface. The sizes of these structures in the pigeon are similar to those observed in the sparrow, the duck and the quail (Röhlich & Vigh, 1967; Mikami, 1975). The protrusions observed in the pigeon are fairly uniform both in shape and in size and we therefore suggest that they all belong to one type. This type of bulbous protrusion belongs to the type I nerve cells described in the sparrow and duck (Röhlich & Vigh, 1967; McNeill et al. 1977) but the pigeon does not appear to have the type II protrusion described by these authors. It is difficult to achieve optimal fixation of the protrusions and it therefore seems possible that open bulbs are not an expression of secretion but represent an artefact caused at the time of dissection after fixation. The cell membrane may become damaged, exposing the cell contents (see also De Waele et al. 1974). The apical poles of the ependymal cells of the

paraventricular organ were obscured by the bulbous protrusions in the pigeon and therefore not visible as in other species (Vigh-Teichman & Vigh, 1983). Nerve fibres, arranged in a flat plexus, have been seen on the paraventricular organ of the chicken (Hirunagi & Yasuda, 1979*b*) but we were unable to find any such fibres in the pigeon. Single fibres, however, might be concealed beneath the closely packed protrusions. Hirunagi & Yasuda (1979*b*) also noted that the fibres they had seen in the chicken were unusual and it might be worthwhile to examine additional animals from this species in order to establish whether the fibres were a chance finding in the 7 animals examined by these authors or whether such fibres are a characteristic of the chicken. The much smaller protrusions of ~ 2.5 μm diameter seem to be too small to be structures belonging to the paraventricular organ. We therefore consider them most likely to be blebs. The functional role of this organ is still a matter of discussion. McNeill et al. (1977) suggested very tentatively that the bulbs might be the morphological correlates of aposecretory mechanisms. De Waele & Dierickx (1979) proposed that the bulbs may 'play a role in the homeostasis of the cerebrospinal fluid' since they are the CSF-contacting dendritic ends of monoaminergic neurons.

The infundibulum

An in-depth comparison between the morphological and functional features of the infundibulum of birds and mammals would alone fill a book. The amount of information collected by SEM in mammals is overwhelming and stands in sharp contrast to the paucity of SEM data in birds and lower vertebrates. Since we have tried to limit our comparisons to structures visible by SEM, this section will be shorter than the reader might expect.

Low-power micrographs of the avian and mammalian mediobasal hypothalamus are remarkably similar in that in both classes the lowest recesses of the 3rd ventricle are almost devoid of cilia (see reviews by Leonhardt, 1980, Mitchell, 1980, and Low, 1982, for information on mammals ranging from marsupials to primates). At higher magnification, however, distinct differences are evident in the ultrastructural composition of the ventricular surfaces (cf. Sharp, 1974). Three different surface patterns were seen in the infundibulum of the pigeon: (1) areas in which there are microvilli, single cilia and numerous head-like protrusions of CSF-contacting neurons; (2) areas in which the cells have only microvilli and long single cilia; and (3) areas in which the cell borders of the ependymocytes are marked with microvilli. According to the anatomical topography of the avian mediobasal hypothalamus (Oksche & Farner, 1974; Kuenzel & van Tienhoven, 1982), the 1st area covers the nucleus of the tuberal region. The 2nd area is very similar to those areas of the subseptal organ and the organum vasculosum of the lamina terminalis that cover the neurohaemal contact zones. It corresponds to the area neurovasculosa of the infundibulum and contains most of the local tanycytes (Matsui, 1966; Sharp, 1972; Oksche & Farner, 1974). The 3rd pattern or type of surface is found within the neurohypophyseal recess itself and is quite similar to the surface pattern seen in the preoptic recess. The occasional single cilia reinforce this impression of similarity although there are major structural and functional differences between the subependymal tissue of the optic recess and that of the neurohypophyseal recess.

The head-like structures seen in the infundibular region of the bird (Vigh-Teichmann et al. 1971; Vigh-Teichmann & Vigh, 1974, 1983) have not been found in this location in mammals. So far the only ependymal areas in which they have been seen in mammals lie within the spinal cord (Rascher et al. 1985). It is generally agreed that these structures are the bulbous ends of dendritic processes, commonly belonging to CSF-contacting neurons (De Waele & Dierickx, 1979; Vigh-Teichmann et al. 1979). They have been thought to be involved in the regulation of CSF ion content or to have an influence on the activity of the median–neurohypophysis eminence complex. An interesting new development in the analysis of the nature of the head-like structures is the finding by Silver et al. (1988) that they are labelled by an antibody to opsin, a substance that also labels rod photoreceptors. It is tempting to speculate whether these CSF-contacting neurons might respond to light and whether they may be phylogenetic remnants of the diencephalic photoreceptive system.

As in the other circumventricular organs, the infundibulum of the pigeon lacked supraependymal or intraventricular nerve fibres. It did, however, have several supraependymal cells.

The infundibular region assumes an important place in neuroendocrine regulation through the median eminence and the neurohypophysis. Studies in the avian brain have shown that diverse interactions between peptidergic and aminergic pathways and the tanycytes take place in the median eminence (Calas, 1975; Mikami, 1975). With morphological criteria as a guideline, 3 different routes of neuroendocrine interaction have been described: (1) the hypothalamo-

adenohypophyseal route, (2) the hypothalamo-neurohypophyseal route, and (3) the tanycytic route. These cells, the tanycytes, are able to take up certain neuropeptides and some tracers after they have been injected into the ventricular system. This ability suggests that tanycytes selectively transport molecules (Calas, 1975; see also Nozaki, 1975). However, a definitive explanation of the function of tanycytes in the infundibular region is not yet available. The rather variable morphology of the tanycyte apical pole might be an expression of the functional state of its basal processes at the time.

The subcommissural organ

This organ has been seen in all vertebrates examined histologically to date and shows the same anatomical relationship to the posterior commissure in both lower and higher vertebrates (Palkovits & Wetzig, 1962). The organ can therefore be considered to be one of the phylogenetically oldest circumventricular organs. The delicate filaments found on its surface represent the secretory product of the organ. The borders of the pigeon subcommissural organ are more richly contoured than those of any of the mammalian organs so far described. The distinct fold of ependymocytes at its anterior end and the elevated ridges or crests along its sides have not been seen in the mammalian subcommissural organ. Supraependymal elements such as free cells and fibres are a common finding on the ependyma surrounding the mammalian subcommissural organ but in the pigeon there were only very few supraependymal elements and these were restricted to the anterior fold. At present we have very little information on the SEM features of the subavian subcommissural organ. De Waele & Dierickx (1979) described the surface of this organ in the frog. It is densely ciliated and has long microvilli but apparently secretory products were not visible on the organ itself. In certain fish, however, filaments of secretory material were clearly discernible and the ultrastructural similarities of the organ with that of the pigeon were remarkable (Kotrschal et al. 1985; Schäfer & Blüm, 1988).

The ependymocytes of the subcommissural organ secrete a mucopolysaccharide (glycoprotein) material that forms delicate filaments on the organ and, further caudally, Reissner's fibre (Meiniel & Meiniel, 1985; Rodríguez et al. 1987). This is a phenomenon that has been found in all animals investigated by SEM to date (Kristic, 1975; Weindl & Schinko, 1977). The secretory activity of the subcommissural organ is unique because even at higher magnifications there does not appear to be any contact between the filaments of secreted material and the cells themselves, nor were any bleb-like structures found. The organ has been implicated in metabolic processes involved in the release of neurotransmitters, especially catecholamines, into the CSF. Reissner's fibre has also been thought to be responsible for trapping particulate matter by adhesion. In our animals the fibre did indeed appear to carry an assortment of particles and an occasional erythrocyte.

The area postrema

The area postrema in both mammals and birds is located in a strategic position at the transition from the ventricular system to the central canal. It is very similar, both in shape and in ultrastructural detail, to this organ in the chicken (Böhme, 1970; Hirunagi & Yasuda, 1979*a*, *b*). The area postrema of these 2 bird species differs more distinctly in its overall shape from that of mammals than any of the other circumventricular organs we have so far compared. This may not be surprising since the contours of the area postrema are remarkably variable from one order of mammals to the next (rabbit: Leonhardt et al. 1975; cat: Leslie et al. 1978). The poorly ciliated surface of the area postrema in the pigeon is sharply delimited from the surrounding densely ciliated nonspecialised ependyma whereas this is not so in all mammals. The rat area postrema has a rather broad transition zone. In mammals the single cilia are usually quite short and the apical poles of the cells are fairly flat. In contradistinction, the pigeon area postrema has remarkably long cilia and the apical poles of the cells are very convex. Its entire surface is more homogeneous than that of mammals. The pigeon area postrema did not bear any supraependymal elements but these have been found in all mammalian organs so far examined.

The area postrema has been related to the control of several visceral reflexes such as emesis and cardiovascular regulation. Feeding and drinking behaviour is evidently influenced by lesions of the area postrema, at least in mammals (Shapiro & Miselis, 1985). In species that normally vomit after ingesting toxins, it has been observed that this response is reduced or refractory if the area postrema is lesioned or destroyed. Considering its complex neuronal connections with the brainstem nuclei and its lack of a blood–brain barrier (Böhme, 1972), the area postrema may be able to modulate interoceptive information from the viscera. Whether the area postrema in birds can also be called a 'chemoreceptor

trigger zone' (Shapiro & Miselis, 1985) needs to be explored. The above-mentioned literature on the avian area postrema does not provide any clues as to its function in this class of vertebrates.

Exceptions to the rules

Areas of ependyma that have been discovered to be specialised histologically (Kuenzel & van Tienhoven, 1982; Korf & Fahrenkrug, 1984) were also examined in the pigeon. Neither the thicker ependyma covering the trochlear nucleus and the medial longitudinal fasciculus nor the ependyma of the lateral ventricles at the level of the septum had any specialisations which could be detected by SEM. Both areas were densely ciliated. Whether this discrepancy is due to species-specific differences or not will remain an open question until additional studies have been completed. Kotrschal et al. (1985) drew attention to this problem after their study of the ventricular system in fish. They stated clearly that there is no 'relationship between the degree of ciliary density and specialized ependyma'. De Waele & Dierickx (1979) have earlier been critical of generalising the connection made between specialisation and lack of dense ciliation.

Supraependymal structures

A very common feature of the mammalian ventricular system is the large number and great diversity of supraependymal structures. Free cells are found on both the specialised and the nonspecialised areas of the ependyma, but are particularly well-documented in the transition zones of the circumventricular organs to their surroundings (Mestres & Breipohl, 1976; Bleier, 1977; Card & Mitchell, 1978; see Jordan & Thomas, 1988, for a review). Most of these cells appear to be macrophages but some have also been identified as neurons. The epiplexus or Kolmer cells are distinct from the other supraependymal cells mainly because they are found on the choroid plexuses (for literature, see Low, 1982; Jordan & Thomas, 1988). It was interesting to discover that the pigeon brain ventricles had only very few supraependymal cells and most of these were epiplexus cells. To our knowledge, there are no reports about the occurrence of supraependymal cells in other bird species. We are unable, therefore, to state whether the paucity of these cells is species-specific or typical of the class Aves. The subavian species described in the literature include reports of large numbers of such cells (reptiles: Bleier, 1977; amphibians: Dellmann, 1978; McKenna & Chairetakis, 1980; Gona & Hauser, 1982; fish: Kotrschal et al. 1985).

The above comparison can be extended to include the occurrence of supraependymal fibres with the one notable exception of networks of fibres of unknown nature on the periventricular organs of the chicken (Hirunagi & Yasuda, 1979). The system of supraependymal fibres has been studied in detail in mammals (Lorez & Richards, 1982; Matsuura et al. 1985). These fibres are for the most part immunoreactive for serotonin. Whether or not the few fibres we found in front of the subcommissural organ are in any way similar to the fibres seen by Ribas (1977) in the epithalamus, we are unable to determine at present.

An unexpected finding

A question that has often been raised by investigators of the CSF spaces is whether or not the posterior telum is fenestrated in birds. Jones & Dolman (1979) were unable to find any such fenestrations or pores. They have been found in amphibians (Jones, 1979) but there are some species of mammals that apparently have no such openings (Oda & Nakanishi, 1987).

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